



# Effects of hyposalinity on survival and settlement of moon jellyfish (*Aurelia aurita*) planulae

Keats Conley\*, Shin-ichi Uye

Graduate School of Biosphere Science, Hiroshima University, 4-4 Kagamiyama 1 Chome, Higashi-Hiroshima 739-8528, Japan



## ARTICLE INFO

### Article history:

Received 1 September 2014

Received in revised form 16 October 2014

Accepted 16 October 2014

Available online xxxx

### Keywords:

Jellyfish

Larvae

Monsoon

Population dynamics

Rainfall

Salinity

## ABSTRACT

Presettlement processes likely influence the geographical distribution and abundance of scyphozoan jellyfish medusae. In East Asian coastal waters, *Aurelia aurita* s.l. spawning coincides with the summer monsoon season, and extreme rainfall events subject planulae to hyposaline conditions, presumably jeopardizing their survival and settlement. In this study, laboratory experiments were conducted to determine how prolonged exposure to hyposalinity (25, 20, and 15, in addition to control salinity 32) affects swimming speed, survivorship and settlement of planula larvae, and subsequent development of metamorphosed polyps. Nearly all planulae ( $\geq 95\%$ ) in 32, 25, and 20 were geonegative during the first 4 h of exposure to respective salinities, but the majority of planulae (70%) in 15 were geopositive. Although no mortality was induced, hyposaline conditions affected larval behavior and the sequence of post-metamorphosis events. Salinity of 15 significantly increased planktonic larval duration and settled polyps had morphological deformities. At a salinity of 20, settled polyps had delayed tentacle development compared to control and 25 treatments. These anomalous results demonstrate that the response of planulae to environmental stress is more complex than previously assumed and may depend on the ability of the settled polyps to develop viable feeding tentacles. Salinity is proposed to be a principal factor influencing planulae dispersion and distribution in temperate monsoon regions.

© 2014 Elsevier B.V. All rights reserved.

## 1. Introduction

The moon jellyfish *Aurelia aurita* s.l. is the most common and abundant scyphozoan in coastal waters of temperate East Asia, including China, Japan, and Korea, and population outbreaks of this species have often caused serious problems in fisheries and coastal power plant operations (Dong et al., 2010; Lee et al., 2006; Mills, 2001; Uye and Ueta, 2004). Genetically, specimens from this region and those from Australia and California, USA, make up a single genotype, temporarily designated as *Aurelia* sp. 1, one of ten *Aurelia* cryptic species (Dawson, 2003; Dawson and Martin, 2001; Ki et al., 2008). In this region, the first problematic bloom of *A. aurita* was reported in Tokyo Bay, where aggregated medusae clogged screens of power plant seawater intakes, resulting in a blackout in the Tokyo metropolitan area in the 1960s (Kuwabara et al., 1969; Matsueda, 1969). Since then, *A. aurita* has become one of the more dominant zooplankton components in Tokyo Bay (Omori et al., 1995; Toyokawa et al., 2000). In the Inland Sea of Japan, a semi-enclosed shallow sea of southwestern Japan, the population of *A. aurita* has significantly increased since the 1980s, based on the results of an extensive poll of fishermen concerning jellyfish population trends and associated nuisance to fisheries (Uye and Ueta, 2004).

Since the 1990s, problematic blooms of *A. aurita* have frequently occurred in both Chinese and Korean coastal waters (Dong et al., 2010; Han et al., 2012; Lee et al., 2006). Environmental and ecosystem changes, such as overfishing, global warming, eutrophication, and marine construction, have been argued as causes for such prominent increases in populations of *A. aurita* in various coastal waters of East Asia (Dong et al., 2010; Uye, 2011). In the context of increasing jellyfish, multiple sectors possess considerable motivation to better predict population fluctuations.

Understanding fluctuations in jellyfish populations is impeded by the complex scyphozoan life history, which consists of a benthic polyp and a pelagic medusa. Medusae sexually produce planulae that settle on hard substrates and metamorphose into polyps, and the polyp stage, in turn, asexually produces new medusae (ephyrae). Interannual fluctuations in abundance of medusae therefore depend upon abundance and survival of each of the life stages of planula, polyp, and ephyra (Schneider and Behrends, 1994). Although the relative influence of mortality at these stages remains unknown, the planula stage determines the polyp stock and therefore may play an important role in medusae abundance, along with the asexual reproduction of settled polyps (e.g. Lucas, 2001). However, comparatively little is known about the physioecology of this larval stage. The planulae of *A. aurita* are lecithotrophic and can persist in the plankton from 1 h to one week (e.g. Gröndahl, 1989; Lucas, 2001; Vagelli, 2007); the duration of the planula stage is hypothesized to depend upon various biotic and

\* Corresponding author at: Department of Biology, 5289 University of Oregon, Eugene, OR 97402, USA. Tel.: +1 208 484 9099.

E-mail address: [keats@uoregon.edu](mailto:keats@uoregon.edu) (K. Conley).

abiotic factors that directly influence swimming behavior and survival in the water column, as well as settling behavior to the substrata (Lucas, 2001; Schneider and Weisse, 1985). More attention has been allocated in determining the role of abiotic factors, including pH, temperature, dissolved oxygen concentration, and salinity (Lucas et al., 2012). The environmental conditions to which planulae are exposed, however, vary among populations. Much of the work on ecophysiology of planulae of *A. aurita* in relation to salinity variations has been modeled on the conditions of the Baltic Sea—the world's largest brackish water system with strong vertical and horizontal salinity gradients (Goldstein, 2012; Holst and Jarms, 2010). The planulae of *A. aurita* in the coastal waters of East Asia experience a different set of environmental conditions, driven by the temperate monsoon climate. This climate regime is characterized by a distinct wet season, in which overturning circulation drives summer monsoon rainfalls (e.g. Trenberth et al., 2000). IPCC models of global climate change in the next century predict that rainfall events in East Asia, including those associated with the monsoon season, will intensify because of the increased atmospheric moisture (Manda et al., 2014). Since the spawning of *A. aurita* in this region coincides with the summer monsoon season, extreme rainfall events subject planulae to hyposaline conditions, which are presumed to jeopardize survival because their physiology may be sensitive to these abrupt salinity reductions.

Responses of the planulae of *A. aurita* have yet to be examined for the environmental conditions imposed by a temperate monsoon regime, where storm surges cause flooding, suddenly exposing medusae and planulae to water of different salinities (e.g. Mills, 1984; Ping and Liu, 1989). We investigated the ecophysiological response, such as swimming behavior, survival, and settlement of planulae, and development of settled polyps, in various hyposalinity conditions.

## 2. Materials and methods

### 2.1. Collection of planulae

Eleven *A. aurita* medusae with planulae observed in brood sacs of the oral arms were collected by a dip net from a pier at Ondo-no-seto (34°11.35' N; 132°32.20' E), central Inland Sea of Japan, on 10 July, 2013. Medusae were kept in lidded buckets filled with filtered (60- $\mu$ m sieve) ambient seawater (salinity: 32) and transported to the Laboratory of Marine Ecosystem Dynamics, Hiroshima University, where they were kept in a temperature-controlled room (24 °C). The next day, medusae incubation water was filtered through a 315- $\mu$ m sieve to remove mucus and gelatinous tissue, and planulae were then concentrated in a 37- $\mu$ m plankton net. This concentrated solution was transferred to a graduated cylinder (1000 ml volume) and left to sit for approximately 30 min to allow planulae to aggregate at the surface and other particulates to settle at the bottom. The planulae were pipetted to a plastic container of filtered (0.2  $\mu$ m) 32-salinity seawater and used in the experiments.

### 2.2. Behavior and survival of planulae at various salinities

As a preliminary experiment demonstrated that all planulae exposed to 10 and 5 salinities had inflated morphology and subsequently disintegrated within 1 h of exposure, four salinity treatments (32, 25, 20, and 15) were tested with twenty replicates per treatment. The 0.2- $\mu$ m-filtered seawater (salinity: 32) from the Ondo-no-seto served as a control, and hyposaline solutions were prepared by adding deionized water of the appropriate ratios to the control seawater. Salinity was measured using a handheld refractometer (Atago Co., Master-S/MillM) with a minimum reading of 1. Eighty polystyrene culture plates, each with 10-ml, 6-wells (diameter: 3.5 cm, depth: 1.5 cm) were prepared, and 10-ml of each of the four salinities was filled in the wells in advance. Then, *A. aurita* planulae were individually

introduced into each well, followed by placement of a 3-cm diameter polyethylene terephthalate (PET) film on the water surface, serving as a settlement plate. The covered culture plates were placed in darkness at 24 °C, reflective of the summer temperature in the Inland Sea of Japan. No food was provided to planulae or polyps.

Following methods similar to Vermeij et al. (2006), periodically (4–24 h intervals) the following parameters were examined for each replicate under a dissecting microscope (Olympus, SZX10): 1) the number of surviving planulae, 2) the position of swimming planulae (surface, column, bottom), 3) the number of settled planulae, and 4) the number of tentacles of metamorphosed polyps. Gently moving the settlement film under the microscope confirmed attachment of planulae to the substrate. To minimize the effect of light exposure, the microscopic observations were shortened, usually  $\leq 5$  min per individual, and the experiment was terminated after 6 d. At the end of the experiment, salinities of ten randomly selected experimental units were tested to confirm that salinity had not changed during the experiment.

To test for the effect of salinity on swimming speed, measurements were conducted for ten randomly selected planulae in salinity of 32, and five randomly chosen planulae in each hyposalinity level after an 8-h exposure to respective salinities. Prior to the measurements, a planula was pipetted with a small volume of water (ca. 0.1 ml), which was spread thinly onto a gridded glass microscope slide with a frame (20  $\times$  50 mm). The horizontal positions of planulae were recorded at 15 frames  $\text{sec}^{-1}$  by a CCD camera (Olympus, DP20) mounted on the microscope, and digitized two-dimensionally using ImageJ (National Institutes of Health, USA) to produce swimming trajectories to calculate the swimming speed of each planula.

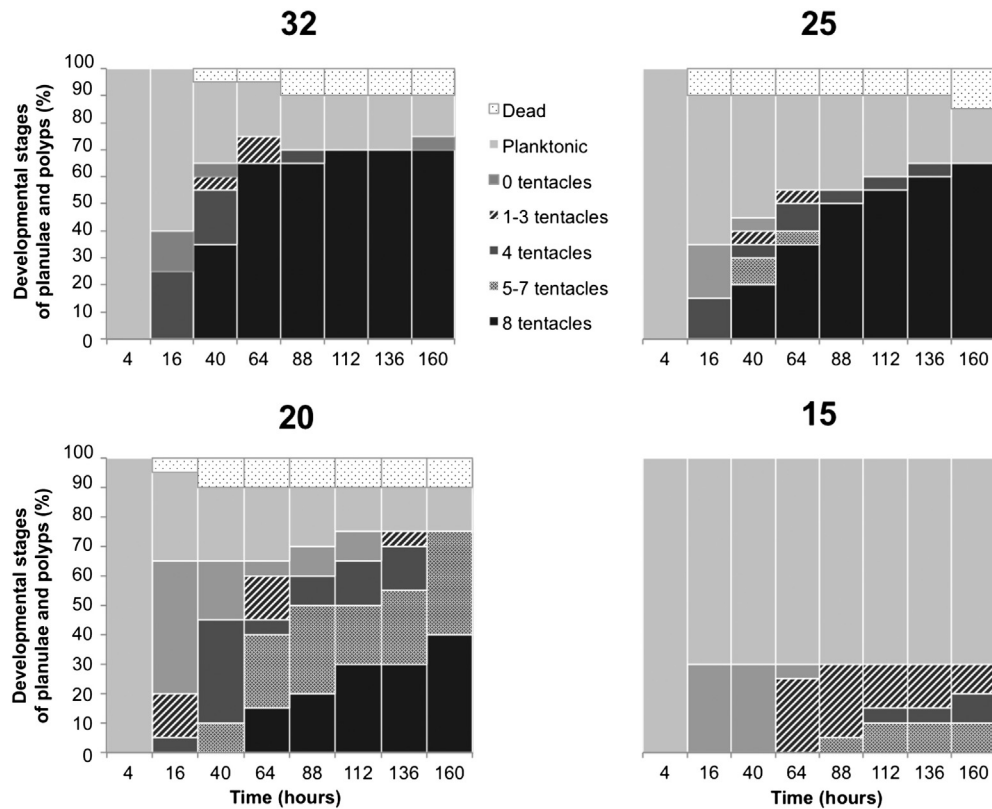
### 2.3. Statistical analysis

In subsequent analysis, the fate of each planula was classified largely to (1) dead, (2) planktonic, and (3) settled and developed (Fig. 1). Since planktonic larval duration (PLD) is a repeated measure of binary outcomes (i.e., planktonic or settled), data were assigned to a time point bin according to time of larval settlement (i.e., larval duration was measured at eight time points during the experiment; if a larva settled at time point 2, it was assigned to bin 2; if a larva remained planktonic at the conclusion of the experiment, it was assigned to bin 8). The effects of salinity on PLD time point bin and morphology (length, width) were tested using one-way ANOVAs. Morphology data adhered to ANOVA assumptions of normality and equality of variance, tested with normal probability plots and Bartlett's tests, respectively. PLD data adhered to assumption of homoscedasticity, but deviated from a normal distribution. However, the ANOVA is quite robust to minor deviations from the assumption of the underlying population's normality (Zar, 1996), and data were also analyzed using the non-parametric Kruskal–Wallis rank sum test for comparison. Swimming speed data violated the assumption of homoscedasticity and could not be corrected with transformations, so was tested using a Kruskal–Wallis one-way ANOVA on ranks, followed by a Nemenyi post-hoc test. All analyses were conducted using R (R Core Team, 2013).

## 3. Results

### 3.1. Survival of planulae

During the course of the experiment, two, three, and two planulae kept at salinities of 32, 25, and 20, respectively, died during pipetting. However, the remaining 73 planulae, even those kept in the 15 treatment, survived the duration of the experiment, indicating that no physiological mortality occurred within this salinity range (Fig. 1).



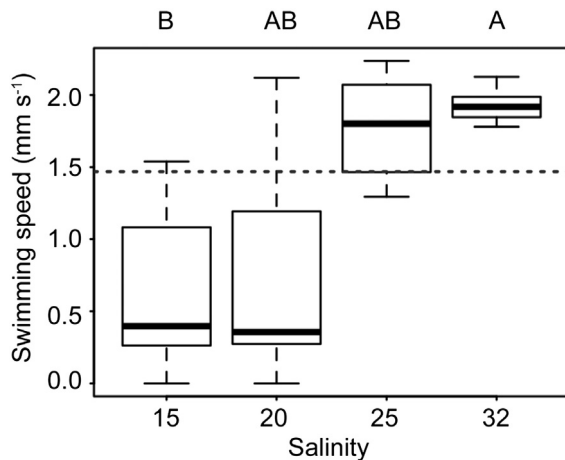
**Fig. 1.** Fraction (%) of swimming planulae (blue) and developmental stage of settled polyps (gray) of *Aurelia aurita* in salinities of 32, 25, 20, and 15 at various elapsed times after the start of the experiment ( $n = 20$  per treatment). Crosshatchings indicate deviations from the normal sequence of tentacle development.

### 3.2. Swimming behavior of planulae

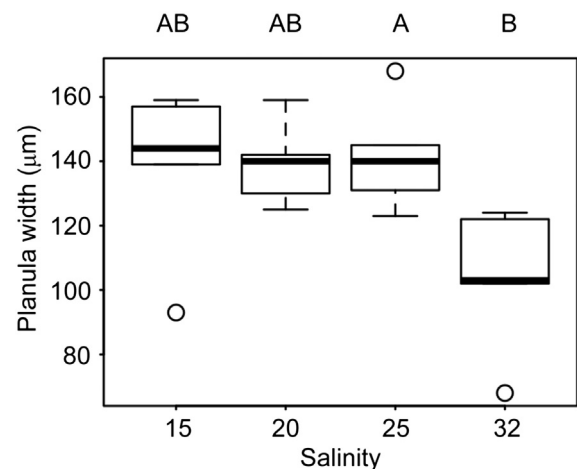
Planulae newly isolated from medusae had mean (SD) long and short diameter of 264 (48) and 130 (21)  $\mu\text{m}$ , respectively ( $n = 10$ ), and swam in smooth and direct trajectories at an average speed of  $1.4 \text{ mm sec}^{-1}$ . This swimming behavior continued for planulae in the control seawater after an 8-h exposure, when their average swimming

speed was  $1.9 \text{ mm sec}^{-1}$  (Fig. 2). Hyposalinity significantly reduced the swimming speed (Kruskal–Wallis chi-squared = 9.473,  $df = 3$ ,  $P = 0.024$ ) as determined for planulae after an 8-h exposure to salinity reductions, where their median swimming speeds reduced by an average of 8, 59, and 66% in 25, 20, and 15 treatments, respectively, compared to those in the control treatment (Fig. 2).

Morphological changes of planulae induced by hyposaline conditions were examined after an 8-h exposure to various salinities. Although there was no significant difference in the long diameter (ANOVA,  $F_{3,16} = 1.67$ ,  $P = 0.213$ ) there was a significant difference in the short diameter for planulae exposed to hyposalinity compared



**Fig. 2.** Median swimming speed of planulae of *Aurelia aurita* 8 h after exposure to salinity treatments ( $n = 10$  at 32, 5 at other salinities). In the boxplots, the box top and box bottom represent the first and third quartile, respectively; the horizontal line in the box shows the median; whiskers show the range. The dashed horizontal line shows the median swimming speed of planulae newly isolated from medusae. The letters A, B, and C indicate significantly different groups with Nemenyi post-hoc test. Any groups sharing the same letter are not significantly different.



**Fig. 3.** Width of planulae of *Aurelia aurita* exposed to salinities of 32, 25, 20, and 15 for 8 h ( $n = 5$  per treatment). In the boxplot, circles beyond the range indicate outliers. The letters A and B indicate significantly different groups with Tukey's HSD post-hoc tests. Any groups sharing the same letter are not significantly different.

to those at salinity 32 (ANOVA,  $F_{3,16} = 3.834$ ,  $P = 0.030$ ) (Fig. 3). Planulae in 20 and 15 treatments exhibited either more round or more elongated body shape than those in 32, and exhibited abnormal swimming behavior, characterized by spiraled motion with occasional immobility.

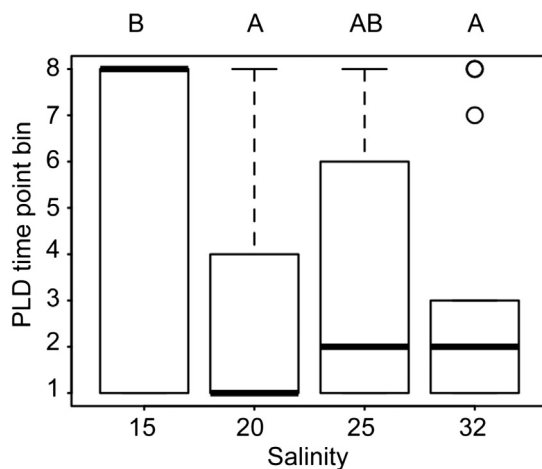
After a 4-h exposure to salinity treatments of 32, 25, and 20,  $\geq 95\%$  of planulae were negatively gravitaxic, since they occupied the air–water interface. In the 15 treatment, 70% of planulae were positively gravitaxic, since they stayed at the bottom of the well.

After 16 h, planulae in the 32, 25, and 20 treatments did not show any apparent behavioral difference from those after an 8-h exposure. However, in the 15 treatment planulae exhibited drastically reduced swimming speeds, and some stayed in the same position, slowly spiraling in a vertical orientation.

### 3.3. Settlement of planulae and development of polyps

The first settlement of planulae occurred within 16 h of incubation in all salinity treatments, and the number of settled planulae increased gradually, except at the lowest salinity of 15, where it remained low, or 30% of initial planulae (Fig. 1). The majority of planulae settled in an inverted position on the underside of the PET film, but 13% of settled planulae in 32 and 50% of settled planulae in 15 attached to the bottom of the well. Salinity had a significant effect on PLD (ANOVA,  $F_{1,72} = 5.089$ ,  $P = 0.003$ ; Kruskal–Wallis chi-squared = 10.1042,  $df = 3$ ,  $P = 0.018$ ), as shown in Fig. 4. Exposure to salinity 15 significantly prolonged PLD, while no significant difference in PLD was found between planulae exposed to 20 and 25 compared to 32. Planulae settled neither on the side of the well nor on the water surface.

Settled planulae metamorphosed to polyps and developed varying numbers of tentacles (Fig. 5). However, polyps exhibited distorted morphologies at salinities  $\leq 20$ . Planulae in 20 settled most rapidly (Fig. 4), but polyps showed delayed and abnormal tentacle development compared to those in 32 and 25 (Fig. 5). Furthermore, at the end of the experiment, 33% of polyps developed only 7 tentacles, whereas no 7-tentacled polyps were observed in salinities above 20. No polyps had developed more than 5 tentacles in 15 at the end of the experiment, and retracted tentacles were more frequently observed at this salinity (Fig. 5).



**Fig. 4.** *Aurelia aurita* median planktonic larval duration (PLD) of planulae exposed to prolonged salinity treatments ( $n = 18, 17, 18$ , and  $20$  at  $32, 25, 20$ , and  $15$ , respectively). Time point bins correspond to time of settlement, where bin 1 indicates settlement within 4 h, bin 2: 16 h, bin 3: 40 h; bin 4: 64 h; bin 5: 88 h; bin 6: 112 h; bin 7: 136 h; bin 8 indicates that the larva remained planktonic at the conclusion of the experiment, 160 h. In the boxplot, circles beyond the range indicate outliers. The letters A and B indicate significantly different groups with Tukey's HSD post-hoc tests. Any groups sharing the same letter are not significantly different.

## 4. Discussion

Herein, salinity has been shown to be an important influence on the planktonic duration of planulae of *A. aurita*, as well as on the subsequent development of metamorphosed polyps. The influence of hyposalinity on planktonic larval duration of cnidarian planulae has been previously established—for example, for Caribbean coral (*Montastraea faveolata*) planulae, whose planktonic larval duration is reduced by decreasing salinity (Vermeij et al., 2006). Our results, however, show that planulae of *A. aurita* exhibit a more dynamic, anomalous response to hyposalinity: salinity of 20 prompted rapid settlement response and reduced PLD, whereas salinity of 15 psu significantly increased PLD. Since salinity is a principal environmental factor affecting critical periods from planktonic life to establishment of benthic polyp populations, it also likely plays a causal role in population fluctuations, dispersion, and distribution.

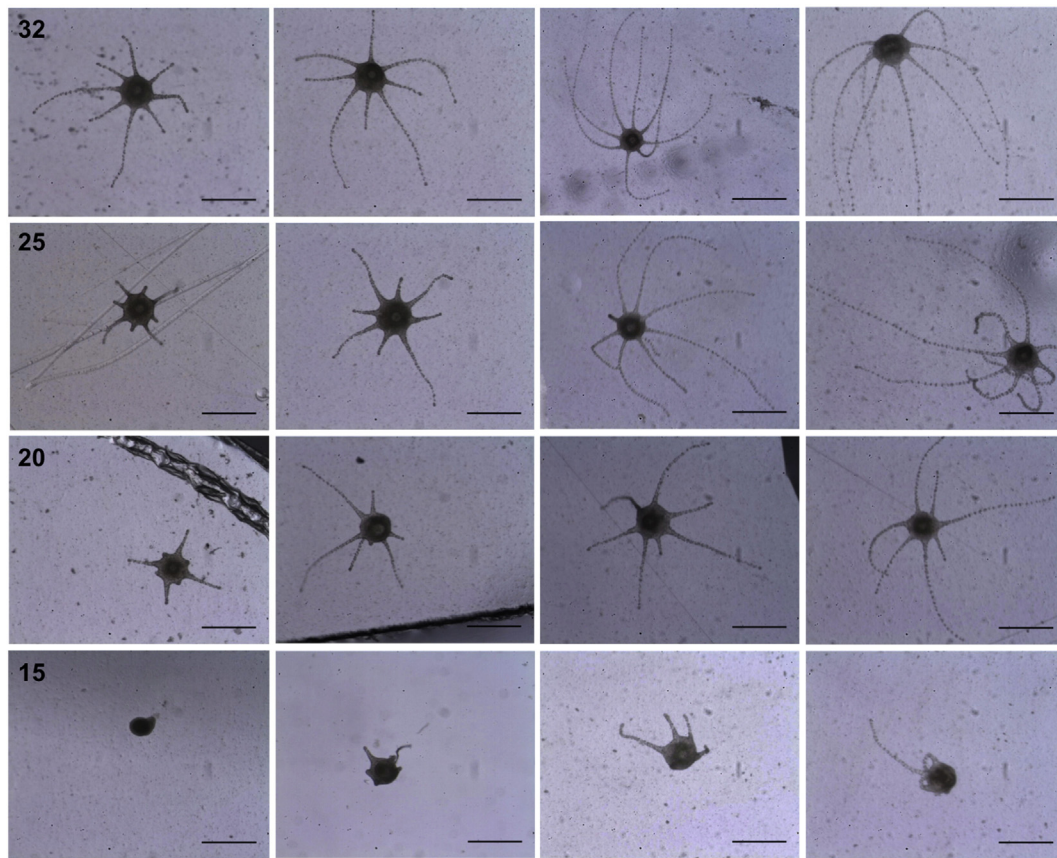
Formation of tentacles during the development of scyphozoan polyps follows a known, sequential spatiotemporal pattern (Yuan et al., 2008). In *A. aurita*, the sequence is 0, 4, 8, 16, and finally 32 tentacles, which radiate symmetrically from the endoderm surrounding the mouth opening (Yuan et al., 2008). Our results show that prolonged exposure (6 d) to salinities  $\leq 20$  caused deviations from the normal sequence of post-metamorphosis events (Figs. 4, 5). Polyps in these hyposaline treatments developed odd numbers of tentacles, which often grew at different rates resulting in pronounced morphological asymmetries. Although the mechanisms by which hyposalinity caused developmental deformities are unknown, such abnormalities presumably reduce polyp survivorship in the long term.

The observed effects of hyposalinity on the physioecology of planulae are ecologically relevant because the salinity range tested in this study reflects natural salinity fluctuations in various East Asian coastal waters. Salinity at the surface layer ( $\leq 0.5$  m deep) along the coast of the Inland Sea of Japan drops below 20 after the heavy rain associated with the warm and wet summer monsoon (Hiroshima Agriculture et al., 2013; Matsuda et al., 1990). Therefore, hyposalinity is presumed to be one of the principal environmental stressors affecting planulae of *A. aurita* in East Asian coastal waters.

### 4.1. Behavior of planulae

While a great deal of attention has been given to the behavior of scyphozoan planulae at the time of settlement (e.g. Brewer, 1976, 1978, 1984; Cargo, 1979; Holst and Jarms, 2007), much less work has described the effect of environmental factors on the swimming behavior of planulae not yet competent to settle (Holst and Jarms, 2010; Prieto et al., 2010). In this study, *A. aurita* planulae avoided swimming in the water column, preferring to swim either at the surface near the settlement film or along the bottom of the well. This observation is in accordance with previous descriptions of behavior of planulae of *A. aurita* from the North Sea (Holst and Jarms, 2007) and is hypothesized to be an adaptive behavior for avoiding turbulence or predation (Webster and Lucas, 2012), or for increasing likelihood of contact with settlement substrates (Holst and Jarms, 2007). The effect of salinity on the geotaxis of planulae is complex; it was negative in 32, 25, and 20, but positive in 15, at least during the first 4 h of exposure. Vermeij et al. (2006) observed a similar response in planulae of *M. faveolata*: the proportion of planulae moving near the bottom of the experimental container increased with decreasing salinity, 36 to 52 h after spawning. This was interpreted to be an adaptive escape response, since, in the field, when a vertical density gradient develops, planulae can escape from a hyposaline surface layer to more saline deep water. Conversely, salinity can impose density differences that may inhibit swimming behavior. Mills (1984) demonstrated that medusae can passively accommodate salinity discontinuities, but that this osmotic accommodation may take up to several hours, and therefore medusae may be unable to cross density gradients that develop suddenly in the field.





**Fig. 5.** Stereo microscopic photographs of juvenile polyp development of *Aurelia aurita* at different salinity levels over time. From left to right: 40 h; 112 h; 136 h; 160 h. Scale bars = 500  $\mu$ m.

This is why mass mortality of the medusae of *A. aurita* occurs after heavy rains in the Inland Sea of Japan (Uye, unpublished).

#### 4.2. Survival of planulae

Planulae are lecithotrophic, and osmotic stress may increase metabolic demand. Under such conditions, planulae may exercise one of two response strategies: 1) remain actively swimming by catabolizing stored energetic reserves within the larval body, awaiting more suitable environmental conditions for settlement and metamorphosis or, 2) settle and metamorphose, which, while potentially energetically costly, enables feeding. Given the responses observed in our study, whether planulae remain swimming or settle may depend on the ability of the settled polyps to develop feeding tentacles. In 20, planulae were able to metamorphose and successfully develop tentacles. Although these polyps developed tentacles more slowly and developed fewer mean number of tentacles compared to 25 and 32, the tentacles ultimately appeared capable of feeding. In contrast, settled planulae in 15 exhibited severe morphological distortions, and feeding tentacles were so stunted or retracted as to prevent proper feeding. Therefore, under severe osmotic stress, extending the planktonic stage may be advantageous compared to metamorphosing into a polyp incapable of feeding itself.

This study shows that the planulae of *A. aurita* from the Inland Sea of Japan are capable of surviving prolonged exposure ( $\geq 6$  d) to hyposaline conditions of 15. Salinity of 10 or lower, however, was fatal to planulae within 1 h of exposure. A tolerance threshold may exist between 10 and 15. These results demonstrate that the planulae of *A. aurita* in the Inland Sea of Japan exhibit a narrower physiological tolerance of low salinity than those in the Baltic Sea. A similar study with planulae of *A. aurita* from the Baltic Sea established 5 as the lower boundary at

which settlement can occur (Goldstein, 2012). At 15, planulae of *A. aurita* from the Inland Sea of Japan exhibit developmental delays similar to those that planulae of *A. aurita* experience in the Baltic Sea at 7.5 (Goldstein, 2012, Fig. 17). Therefore, physiological tolerances differ at the population level in addition to the species level.

The vast majority of experiments with planula larvae use experimental designs wherein multiple larvae occupy a single replicate (e.g. Duarte et al., 2012; Vermeij et al., 2006; Webster and Lucas, 2012). This design is often justified on the basis that larvae exhibit high mortality rates, and therefore multiple larvae may be necessary to obtain sufficient results. It is problematic, however, because it treats non-independent samples as true replicates and permits confounding interaction effects within treatments, such as gregarious behavior (e.g. Gotelli, 1990; Gröndahl, 1989) and cannibalism (Gröndahl, 1988). In a pre-experiment trial with multiple larvae occupying one container, newly settled polyps were observed to cannibalize the swimming planulae, which could confound the settlement ratios of planulae. Our results demonstrate that it is feasible to conduct experiments using only one planula per replicate. Under laboratory conditions, planulae were found to exhibit high survival rates. In the field, too, lecithotrophic larvae such as cnidarian planulae are presumed to have lower mortality rates than planktotrophic larvae of echinoderms because of their shorter development time (Lucas et al., 2012; Uthicke et al., 2009). This design may therefore be used in future planulae experiments to reduce confounding variables inherent in laboratory studies that use multiple larvae per replicate.

The accepted value for the survival period of *A. aurita* planulae is up to one week (e.g. Gröndahl, 1989; Lucas, 2001; Vagelli, 2007). Based on C, N, P contents and metabolic measurements such as respiration and excretion, the maximal duration of the free-swimming planula stage has been estimated to be between days and one week

(Schneider and Weisse, 1985). In a pre-experiment trial, planulae in experimental containers without floating substrates were observed to survive considerably longer than this—capable of active swimming for up to three weeks. This observation is more in line with the survival period estimated for *Cyanea capillata* planulae, which can remain swimming for up to one month (Russell, 1970). Swimming duration presumably depends on multiple environmental factors, including temperature, water turbulence, and presence of suitable settlement substrate, but our laboratory observations suggest *A. aurita* planulae may be capable of considerably postponing metamorphosis. If planulae do, in fact, prolong their larval period in the field to the same extent as observed in the laboratory, and if these larvae retain the ability to settle and metamorphose, this could have implications for dispersal of the benthic polyp stock (e.g. Pechenik, 1990).

## 5. Conclusions

This study is a first step toward understanding how the physical factors reflective of a temperate monsoon regime affect the behavior and survival of planulae of *A. aurita* s.l. Our results demonstrate the importance of salinity on larval settlement and subsequent development of polyps, which, in turn, could play an important role in defining polyp abundance and strobilation rates.

## Acknowledgments

We would like to thank Mariko Takao and Ryuji Furukawa for their assistance in field sampling and the laboratory experiment. We would also like to thank Kelly Sutherland and the anonymous reviewers for providing constructive feedback on the manuscript. This material is based upon work supported by the Japan Society for the Promotion of Science under Grant No. OISE-1316427 and the National Science Foundation under Grant No. OISE-1316427 for an East Asia and Pacific Summer Institutes for U.S. Graduate Students (EAPSI) fellowship. [SS]

## References

- Brewer, R.H., 1976. Larval settling behavior in *Cyanea capillata* (Cnidaria: Scyphozoa). *Biol. Bull.* 150, 183–199.
- Brewer, R.H., 1978. Larval settlement behavior in jellyfish *Aurelia aurita* (Linnaeus) (Scyphozoa, Semaestomeae). *Estuaries* 1, 120–122.
- Brewer, R.H., 1984. The influence of the orientation, roughness, and wettability of solid surfaces on the behavior and attachment of planulae of *Cyanea* (Cnidaria: Scyphozoa). *Biol. Bull.* 166, 11–21.
- Cargo, D.G., 1979. Observations on the settling behavior of planular larvae of *Chrysaora quinquecirrha*. *Int. J. Invertebr. Reprod.* 1, 279–287.
- R Core Team, 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, (<http://www.R-project.org/>).
- Dawson, M.N., 2003. Macro-morphological variation among cryptic species of the moon jellyfish, *Aurelia* (Cnidaria: Scyphozoa). *Mar. Biol.* 143, 369–379.
- Dawson, M.N., Martin, L.E., 2001. Geographic variation and ecological adaptation in *Aurelia* (Scyphozoa, Semaestomeae): some implications from molecular phylogenetics. *Hydrobiologia* 451, 259–273.
- Dong, Z., Liu, D., Keating, J.K., 2010. Jellyfish blooms in China: dominant species, causes and consequences. *Mar. Pollut. Bull.* 60, 954–963.
- Duarte, C.M., Pitt, K.A., Lucas, C.H., Purcell, J.E., Uye, S.I., Robinson, K., Brotz, L., Decker, M.B., Sutherland, K.R., Malej, A., Madin, L., Mianzan, H., Gili, J., Fuentes, V., Atienza, D., Pagés, F., Breitbart, D., Malej, J., Graham, W.M., Condon, R.H., 2012. Is global ocean sprawl a cause of jellyfish blooms? *Front. Ecol. Environ.* 11, 91–97.
- Goldstein, J., 2012. Ecophysiological Experiments With Polyps of *Aurelia aurita* and *Cyanea capillata* (Scyphozoa, Cnidaria) (M.S. Thesis) Universität Rostock, Rostock, Germany.
- Gotelli, N.J., 1990. Stochastic models of gregarious larval settlement. *Ophelia* 32, 95–108.
- Gröndahl, F., 1988. Interactions between polyps of *Aurelia aurita* and planktonic larvae of scyphozoans: an experimental study. *Mar. Ecol. Prog. Ser.* 45, 87–93.
- Gröndahl, F., 1989. Evidence of gregarious settlement of planula larvae of the scyphozoan *Aurelia aurita*: an experimental study. *Mar. Ecol. Prog. Ser.* 56, 119–125.
- Han, C.H., Chae, J., Jin, J., Yoon, W., 2012. Estimation of the minimum food requirement using the respiration of medusa of *Aurelia aurita* in Sihwa Lake. *Ocean Sci. J.* 47, 155–160.
- Hiroshima Agriculture, Forestry, Research, Fisheries, Center, Development, 2013. "Temperature and Salinity of the 2012 Hiroshima Bay", (<http://www.haff.city.hiroshima.jp/suisanso/12suion.html>) (In Japanese) (accessed 27 August, 2014)).
- Holst, S., Jarms, G., 2007. Substrate choice and settlement preferences of planula larvae of five Scyphozoa (Cnidaria) from German Bight, North Sea. *Mar. Biol.* 151, 863–871.
- Holst, S., Jarms, G., 2010. Effects of low salinity on settlement and strobilation of scyphozoa (Cnidaria): is the lion's mane *Cyanea capillata* (L.) able to reproduce in the brackish Baltic Sea? *Hydrobiologia* 645, 53–68.
- Ki, J.S., Hwang, D.S., Shin, K., Yoon, W.D., Lim, D., Kang, Y.S., Lee, Y., Lee, J.-S., 2008. Recent moon jelly (*Aurelia* sp.) blooms in Korean coastal waters suggest global expansion: examples inferred from mitochondrial COI and nuclear ITS-5.8S rDNA sequences. *ICES J. Mar. Sci.* 65, 443–452.
- Kuwabara, R., Sato, S., Noguchi, N., 1969. Ecological studies on the medusa, *Aurelia aurita*. 1. Distribution of *Aurelia* patches in the north-eastern region of Tokyo Bay in summer of 1966 and 1967. *Bull. Jpn. Soc. Fish. Oceanogr.* 35, 156–162 (in Japanese with English abstract).
- Lee, J.H., Choi, H.W., Chae, J., Kim, D.S., Lee, S.B., 2006. Performance analysis of intake screens in power plants on mass impingement of marine organisms. *Ocean Polar Res.* 28, 385–393.
- Lucas, C.H., 2001. Reproduction and life history strategies of the common jellyfish, *Aurelia aurita*, in relation to its ambient environment. *Hydrobiologia* 451, 229–246.
- Lucas, C.H., Graham, W.M., Widmer, C., 2012. 3 Jellyfish life histories: role of polyps in forming and maintaining scyphomedusa populations. *Adv. Mar. Biol.* 63, 133.
- Manda, A., Nakamura, H., Asano, N., Iizuka, S., Miyama, T., Moteki, Q., Yoshioka, M.K., Nishii, K., Miyasaka, T., 2014. Impacts of a warming marginal sea on torrential rainfall organized under the Asian summer monsoon. *Sci. Rep.* 4, 1–6.
- Matsuda, O., Kishimoto, Y., Hamasaki, S., 1990. Factors affecting seasonal variation of oceanographic conditions at Kure port. *J. Fac. Appl. Biol. Sci.* 29, 135–144 (In Japanese with English abstract).
- Matsueda, N., 1969. Presentation of *Aurelia aurita* at thermal power station. *Bull. Mar. Biol.* 13, 187–191.
- Mills, C.E., 1984. Density is altered in hydromedusae and ctenophores in response to changes in salinity. *Biol. Bull.* 166, 206–215.
- Mills, C.E., 2001. Jellyfish blooms: are populations increasing globally in response to changing ocean conditions? In: Purcell, J.E., Graham, W.M., Dumont, H.J. (Eds.), *Jellyfish Blooms: Ecological and Societal Importance*. Springer, Netherlands, pp. 55–68.
- Omori, M., Ishii, H., Fujinaga, A., 1995. Life history strategy of *Aurelia aurita* (Cnidaria, Scyphomedusae) and its impact on the zooplankton community of Tokyo Bay. *ICES J. Mar. Sci.* 52, 597–603.
- Pechenik, J.A., 1990. Delayed metamorphosis by larvae of benthic marine invertebrates: does it occur? Is there a price to pay? *Ophelia* 32, 63–94.
- Ping, L.N., Liu, C.G., 1989. Effect of salinity on larva of edible medusae (*Rhopilema esculenta* Kishinouye) at different development phases and a review on the cause of jellyfish resources falling greatly in Liaodong Bay. *J. Acta Ecol. Sin.* 4, 3.
- Prieto, L., Astorga, D., Navarro, G., Ruiz, J., 2010. Environmental control of phase transition and polyp survival of a massive-outbreaker jellyfish. *PLoS One* 5, e13793.
- Russell, F.S., 1970. The Medusae of the British Isles. II. Pelagic Scyphozoa With a Supplement to the First Volume on Hydromedusae. Cambridge University Press, Cambridge (281 pp.).
- Schneider, G., Behrends, G., 1994. Population dynamics and the trophic role of *Aurelia aurita* medusae in the Kiel Bight and western Baltic. *ICES J. Mar. Sci.* 51, 359–367.
- Schneider, G., Weisse, T., 1985. Metabolism measurements of *Aurelia aurita* planulae larvae, and calculation of maximal survival period of the free swimming stage. *Helgol. Mar. Res.* 39, 43–47.
- Toyokawa, M., Furota, T., Terazaki, M., 2000. Life history and seasonal abundance of *Aurelia aurita* medusae in Tokyo Bay. *Biol. Ecol.* 47, 48–58.
- Trenberth, K.E., Stepaniak, D.P., Caron, J.M., 2000. The global monsoon as seen through the divergent atmospheric circulation. *J. Clim.* 13, 3969–3993.
- Uthicke, S., Schaffelke, B., Byrne, M., 2009. A boom-bust phylum? Ecological and evolutionary consequences of density variations in echinoderms. *Ecol. Monogr.* 79, 3–24.
- Uye, S.I., 2011. Human forcing of the copepod–fish–jellyfish triangular trophic relationship. *Hydrobiologia* 666, 71–83.
- Uye, S.I., Ueta, Y., 2004. Recent increase of jellyfish populations and their nuisance to fisheries in the Inland Sea of Japan. *Bull. Jpn. Soc. Fish. Oceanogr.* 68, 9–19.
- Vagelli, A., 2007. New observations on the asexual reproduction of *Aurelia aurita* (Cnidaria, Scyphozoa) with comments on its life cycle and adaptive significance. *Invertebr. Zool.* 4, 111–127.
- Vermeij, M.J.A., Fogarty, N.D., Miller, M.W., 2006. Pelagic conditions affect larval behavior, survival, and settlement patterns in the Caribbean coral *Montastraea faveolata*. *Mar. Ecol. Prog. Ser.* 310, 119–128.
- Webster, C.N., Lucas, C.H., 2012. The effects of food and temperature on settlement of *Aurelia aurita* planula larvae and subsequent somatic growth. *J. Exp. Mar. Biol. Ecol.* 436, 50–55.
- Yuan, D., Nakanishi, N., Jacobs, D.K., Hartenstein, V., 2008. Embryonic development and metamorphosis of the scyphozoan *Aurelia*. *Dev. Genes Evol.* 218, 525–539.
- Zar, J.H., 1996. *Biostatistical Analyses*, 5th ed. Prentice Hall, Upper Saddle River, NJ.